

# Moose anti-predator behaviour towards baying dogs in a wolf-free area

Göran Ericsson<sup>1</sup>  · Wiebke Neumann<sup>1</sup> · Holger Dettki<sup>1</sup>

Received: 7 August 2014 / Revised: 13 May 2015 / Accepted: 14 May 2015 / Published online: 27 May 2015  
© Springer-Verlag Berlin Heidelberg 2015

**Abstract** Understanding the impact of human activity on prey anti-predator behaviour is becoming increasingly important. For many species, hunting is the dominating mortality cause in areas where predators are functionally extinct. In a controlled field experiment in Northern Sweden devoid of wolves, we exposed adult female moose (*Alces alces*) to hunting activity using a dog (*Canis lupus familiaris*) to study individual moose anti-predator behaviour. Moose were more active, had larger 24-h activity ranges and left the area after the disturbance. Our study supports the existence of several anti-predator strategies within a species even when predators are absent. A mixed strategy among individuals may be beneficial when a new predator eventually enters the system. Instead of fronting as expected from other study systems, most individuals fled when confronted. We argue that heavily harvested Scandinavian moose may be more adapted to human and bear predation in contrast to the suggested behavioural maladaptation towards wolf predation. We build on two major lines of arguments; first, being less defensive, but fleeing when approached by a baying dog which mimics wolf encounters, is likely to increase moose survival compared with the risk to be shot when being defensive and fronting, held at bay. Secondly, we assume that escaping in a tortuous manner, i.e. in an unpredictable way, may increase the chance to undergo persecution by increasing the chance that chaser switches the target animal, especially in areas of high moose

density. We recommend future studies to address individual variation and behavioural plasticity in anti-predator behaviour.

**Keywords** Disturbance · Individual-based experiments · *Alces alces* · Sweden · Vigilance

## Introduction

Wild animals use a range of behavioural responses to escape predation and reduce the risk of being killed. Prey show predator-specific adjustments to the most abundant predator, including humans (Lima 1992; Proffitt et al. 2009). Well-known examples of suggested predator-specific adjustments are elk (*Cervus elaphus*) habitat response to recolonizing wolves (*Canis lupus*) (Christiansson and Creel 2008), moose behavioural adjustment to recolonizing brown bear (*Ursus arctos*) (Berger et al. 2001) and differential anti-predator responses such as vigilance and visitation duration to predators with differing hunting modes in red deer (*C. elaphus*; Wikenros et al. 2015).

Environmental characteristics like openness of the landscape and topography may also affect prey response to predator presence. In closed and complex landscapes like the boreal forest, it is harder to keep groups together; prey there tend to live solitary or shift habitat to reduce the success of a stalking predator (Atwood et al. 2009). Therefore, we can expect in closed and dense forests that the physical landscape affects the fine-scale predation risk by pursuit predators, increasing the importance of indirect effects like reduced browsing intensity in wolf core areas with a large amount of coarse woody debris (Kuijper et al. 2013).

Increased vigilance is a context-dependent anti-predator strategy that comes with increased predation risk with (Eisenberg et al. 2014). Using the strategy to flee, outrun

---

Communicated by P. Acevedo

✉ Göran Ericsson  
goran.ericsson@slu.se

<sup>1</sup> Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden

and/or confuse the attacker is often used when the predators are inexperienced, few or when conditions are favourable or predators are spotted before they discover the prey (Caro et al. 2004; Ballard and Van Ballenberghe 2007; Samia et al. 2013).

In closed vegetation, an attacker like wolves cannot rely on vision solely to detect its prey; it may be then advantageous to confuse the predator. Thus, to escape in a tortuous path can be strategic as it enables the prey to detect and control the approach of a stalking predator (Jarnemo and Wikenros 2014). Previous studies clearly demonstrate that deer species do adjust their behaviour to predator presence as species change their diurnal activity pattern, move faster and more erratic when faced with the risk of predation (Cederlund and Kjellander 1991; Baskin et al. 2004; Stankowich 2008).

An alternative strategy for the prey is to stay and to confront the attacker. When attacked by wolves, e.g. moose may front the attackers which often enhance survival (Ballard and Van Ballenberghe 2007). Moose are quite often successful in fighting wolves of small packs and when, e.g. snow conditions are favourable (Mech 1966; Peterson et al. 1984).

Inferring from natural interactions with predators, we anticipate behavioural adjustments in prey species when either a new predator enters or leaves the system (Berger 2007). Previous research shows that when the predation pressure is relaxed, prey species adjust accordingly (Creel et al. 2008). Prey behavioural adjustments also include predation risk by humans (Proffitt et al. 2009). Humans have the last centuries played a role here by actively removing and sometimes eventually driven predators to extinction. Wolves are examples of this both in North America and Europe.

In Scandinavia, hunting has replaced wolf predation along with the strong comeback of large deer prey species like moose the last 50 years (Danell and Bergström 2009). In Sweden, wolves were already in the 1860s functionally extinct from vast areas of Sweden and started first by 1990 to slowly return in any noticeable numbers to Sweden (Wabakken et al. 2001). Today, there are still just some 350 wolves (Swedish EPA 2014a) and 2800 bears (Swedish EPA 2014a) in Sweden (495,000 km<sup>2</sup>). Bears were also functionally extinct from vast areas of Sweden until the 1990s (Swenson et al. 1994). Thus, hunting replaced natural predation as the dominating mortality factor already during the nineteenth century since then relaxed for many, many moose generations.

Moose in Sweden are now facing recolonizing wolves again after wolf predation pressure has been relaxed for centuries (Wabakken et al. 2001; Nicholson et al. 2014). Thus, the currently evolved anti-predatory strategies addressing human hunting may affect moose anti-predator behaviour when human and wolf predation strategies overlap (Sand et al. 2006; Wikenros et al. 2009).

Dogs have always been an important part of Scandinavian hunting as trackers aiding the human hunters, but with the disappearance of wolves, hunters already some 200 years

ago developed a new hunting behaviour without risking the dog to be killed by wolves. Consequently, in Scandinavia and in the absence of wolves, hunting dogs like Norwegian Elkhounds (*C. lupus familiaris*) increasingly progressed in to hold their target game at bay when hunting moose or even small game like grouse (Lavsund et al. 2003). Hunters train their moose-baying dogs to utilize the moose defence strategy of moose fronting their attacker like wolves. When hunted by humans, this is maladaptive due to the high likelihood of being shot while fronting the baying dog. When at bay, the dog starts to bark, moose continue to front the dog which allows the hunter to approach the animals, using vegetation cover and moving against the wind.

So what happens when wolves return and humans continue using baying dogs? Although moose is the dominant prey for Scandinavian wolves, hunting is the major source of moose mortality even in wolf territories (Sand et al. 2006, 2008). In the 13–16 south-central Swedish territories studied by Sand and co-workers, moose did show less aggressive behaviour compared with their North-American counterparts and commonly fled when confronted (Sand et al. 2006; Wikenros et al. 2009). Previous studies speculate if this is a result of the history of hunting with dogs in the absence of wolves (ibid). In short, can the hunting success of recolonizing wolves be a result of naive moose that over generations have undergone a behavioural adjustment, being less defensive and more prone to escape rather than fronting their attacker as their North-American counterparts do (Wabakken et al. 2001; Sand et al. 2006; Wikenros et al. 2009)? While Scandinavian moose within one generation behaviourally adjust to recolonizing brown bear predation and become more aggressive, more likely to fight of an attacker and use alternate habitats (Berger et al. 2001), Sand and co-workers suggest that sufficient moose behavioural adjustments to reduce predation by wolves are still lacking (Sand et al. 2006). However, no data from controlled situations actually exists if and how moose defence varies among individuals.

Previous studies have been performed in areas where wolves were already established and not with an experimental approach. In our pilot study, we test the spatiotemporal response of Swedish female moose to a moose-baying dog in an area that is and has been free of wolf predation at least the last 100 years (Wabakken et al. 2001). We used free-ranging moose in an individual-based experimental design. Based on theory and our review of the literature, we expect that Scandinavian moose in wolf-free areas have undergone alteration in anti-predator behaviour addressing dominantly human predation, i.e. showing no defence behaviour but high disposition to escape. Thus, we predict that moose in wolf-free areas will (1) flee when approached by a hunting dog, and (2) escape from the persecuting hunting dog by moving in a tortuous manner. We furthermore expect moose to display (3) greater movement activity when exposed to hunting activity

and (4) enlarged 24-h activity range, which results in spatial displacement.

## Material and methods

After WWII, moose are annually hunted throughout Sweden with a harvest of approximately up to one third of the winter population annually from the late 1960s and on (SOU 2009), resulting in a high population turnover (Lavsund et al. 2003). Compared with densities in Canada and North America (Ripple and Betscha 2012), Swedish moose densities are higher (Lavsund et al. 2003). Currently, the winter density before annual reproduction is around 1 moose/km<sup>2</sup> nationally but varies from <0.1 moose/km<sup>2</sup> to >2 moose/km<sup>2</sup> (SLU 2014). The annual harvest fluctuate around 100,000 moose a year. There are some 300,000 hunters in Sweden (Swedish EPA 2014b), and 40 % of them are also dog owners.

We performed the study during August and September 2006 with a total length of the experimental period of 21 days, just before the onset of the annual hunt.

## Study area

Our study area ranged from interior boreal forest to low alpine forests in northern Sweden where moose migrate to mountainous summer season areas and to boreal forest in winter (Singh et al. 2012). The interior (64° 26' N 19° 22' E, WGS84) is dominated by Scots Pine (*Pinus sylvestris*), covering a gently rolling landscape with an average elevation of 309±5 m (mean±SE). Human density is low, averaging 2 humans/km<sup>2</sup>, while accessibility is moderate with 1.0 km/km<sup>2</sup> (Statistics Sweden 2008; Swedish Land Survey 2008). Boreal and mountainous birch forest dominate the low alpine area (65° 42' N 16° 46' E, WGS84), partly above tree line. Elevation averages 996±11 m (mean±SE), and both human density and accessibility are very low (0.4 humans/km<sup>2</sup>, 0.4 km/km<sup>2</sup>; Statistics Sweden 2008; Swedish Land Survey 2008).

In our study area, the hunting season starts in the beginning of September and lasts until the end of December for adult moose. Calves can also be harvested until January. Moose are harvested on annual quota system based on acreage controlled or leased by the collective hunting groups. Harvest of calves is not regulated and completely open in terms of numbers. The study area is in the region of Västerbotten where there are some 18,900 hunters, which gives an average density of 0.3 hunters/km<sup>2</sup> land area (Swedish EPA 2014b). The mortality risk from natural predators such as brown bears is low (0.005 bears/km<sup>2</sup>), particularly for adult moose (Swenson et al. 2007; Swedish EPA 2014a). Wolves were absent from our study area, except single stray individuals dispersing (Swedish EPA 2014a). Aerial surveys had previously

estimated the moose density to 0.7 moose/km<sup>2</sup> in 2006 (Eric's BioJobtjänst 2006).

## Experimental protocol

We compared moose relative response among three trials to evaluate moose behaviour to repeated exposure to hunting activity. Regular hunting activity in the area restricted the timing of our experimental approaches, resulting in interval differences with 7±0.3 days SD between the two first repetitions and 29±3 days SD between the second and third one. To avoid regular moose-hunting activity, the third approach had to be placed into the official break of the regular moose hunt after the 25th of September.

Ten female moose was previously immobilized from a helicopter using a dart gun to inject a mixture of an anaesthetic and a tranquilizer (etorphine and xylazine; Kreeger and Arnemo 2007) and equipped with a collar that included a global positioning system (GPS) receiver, global system for mobile communication (GSM) modem and a traditional VHF beacon (Vectronic Aerospace GmbH, Berlin, Germany). On the day of experimental disturbance, the day before and after, the collar calculated a position every 10 min. To assess the effect of reproductive status on moose response, half of the females included in the experiment were accompanied by calves ( $n=5$ ) and half were barren ( $n=5$ ). Tooth wear indicated an average female age of 7±3 years SD, an age class with the lowest risk to be harvested by hunters due to its high reproductive potential (Solberg et al. 2000; Ericsson and Wallin 2001).

Treatments started on the first day of legal dog training on the 21st of August. The use of baying dogs is the dominating form of hunting and therefore assumed all animals in the experiments to have hunting experience, i.e. being non-naïve, though to an unknown extent. If familiarization to hunting activity would take place, we expected moose to be less sensitive at our third approach. All moose were assigned three experimental trails. Using the last known GPS position and the VHF beacon, we approached moose and let the dog off the leash at a distance of 90±52 m (mean±SD) to the moose. The distance calculated post-trail on site. Mimicking normal moose hunting, we moved silently, using the vegetation as cover, against the wind to enable the dog to scent the moose in closed terrain and to any confounding effect of human disturbance. When the dog signalled that it scented the target animal, we silently off-leashed it out of site from the moose position.

The dogs were Norwegian elkhounds which is the most common breed used for moose hunting in Northern Europe. Due to forest road closures, two moose failed to be disturbed three times, resulting in 28 experimental approaches of which 24 were carried out by the same dog. Two additional dogs

were used the remaining four trials due to logistic problems. The dogs were equipped with a GPS with constant tracking.

At the site of moose-dog contact, we recorded air temperature, precipitation (type and strength), wind (strength and direction) and habitat type. The position of contact was when the dog most likely where in contact with the target animal. To assess moose perception of risk, we noted the moose's initial response towards the approaching dog.

The project was approved by the Animal Care Committee for Northern Sweden in Umeå (Dnr A124-05 2005-11-15) and was carried out in accordance with the Swedish laws concerning animal research ethics. All personnel were certified according to the standards by the SLU, the Swedish Animal Welfare Agency and the Swedish Board of Agriculture.

### Statistical analysis

For each individual, we calculated the distance in metres from the previous position using Euclidean distance and computed “speed” (m/h). To assess the relative response, we compared the calculated speed during the hours following disturbance with the individual's speed during the same circadian period the previous 24 h using the Wilcoxon signed-rank test. Each individual was used as its own control for individual's difference in moose circadian rhythm.

We calculated 24-h activity ranges for the day of treatment and daily before and after (Ranges 6 v1. 217, Anatrack Ltd. Wareham, UK) to explore moose space use. Here, we calculated fixed 95 % kernels with selected cores using least squares cross validation to estimate the smoothing factor, based on  $90 \pm 0.6$  (mean  $\pm$  SE) fixes per range. We used a linear-mixed model with moose individual as a random factor, and a repeated statement using Kenward-Roger correction and adjusted *p* values given by Tukey post hoc test to explore differences among range sizes among disturbance trails (Littell et al. 2006). To test if moose left the area of disturbance, we compared the overlap (%) of the ranges as well as distance (m) between the centroids of the pre- and post-treatment diurnal ranges using the Wilcoxon signed-rank test. We evaluated moose displacement over time and among treatment trials by calculating the linear distance of moose position to the initial disturbance position at the 6th, 12th, 18th, 24th, 48th and 72nd hour following disturbance using a linear-mixed model with repeated measures.

We assessed differences in dog tracking effort among trials using a linear-mixed model with repeated measures. We used the non-parametric Cochran Q test to address whether frequency of initial moose response towards the approaching hunting dog, i.e. risk assessment, differed among trials (escape immediately; escape after hold at bay less than 5 min; moose stands at bay more than 5 min).

Escape behaviour was analysed by calculating the ratio of the linear distance to the sums of cumulative distances moose had moved to their resettle point. For moose that left the area by moving directly to its resettle point, the ratio would be 1, while it would be smaller than 1 for a tortuous escaping path. We tested for difference between linear and cumulative distances moved using the Wilcoxon signed-rank test. We assumed the shape of escape path to be an index of risk assessment, likewise as moose initial response (Stankowich and Coss 2007; Stankowich 2008).

Secondly, we evaluated the factors potentially affecting moose escape behaviour. We transformed the shape of moose escape path using the arcsine transformation as recommended for proportion data (Crawley 2007). We evaluated moose escape pattern with respect to dog, moose and environmental parameters (i.e. dog tracking time; distance at which the dog left off-leash; moose age; moose reproductive status; time until moose resettled) using linear-mixed models with repeated measures and moose as random effect. We assumed moose age to represent an index of non-naivety with older moose having more hunting experiences. Because dog tracking effort and time until moose resettled were highly correlated (correlation=0.87), we continued our analysis without the term “time until moose resettled”. Due to the sample size, we tested only univariate models and selected the best-supported model using the Akaike's information criterion (AIC) (Burnham and Anderson 2002). We explored the variance in moose escape path explained by the different moose individuals using variance component analysis (Crawley 2007).

We used the software ArcGIS 9.2 (ESRI, Redlands, CA, USA) for all GIS analyses, SAS 9.1.3 (SAS Institute Inc. Cary, NC, USA) and open-source programme R 2.11.1 for statistical computing, and set the significance level to  $<0.05$ . If necessary, data was log-transformed. When transformation failed to produce normality, we used non-parametric tests, e.g. the Wilcoxon signed-rank test. Covariance decreased with time so we applied the first-order autoregressive covariance structure with assignment to account for unequally spaced intervals in our linear-mixed models with repeated measures (Littell et al. 2006).

### Results

In line with our first prediction, moose fled in 80 % (23 of 28 approaches) of all dog contacts. Of the remaining five approaches, three moose stood at bay  $<5$  min, and two moose stood  $>5$  min. Thus, moose showed a mixed response with one dominating strategy.

Supporting our second prediction for closed habitats, the escape paths were tortuous and moose moved twice as much as the linear distance to its resettle position  $3.1 \pm 0.4$  km (mean  $\pm$  SE) apart from the disturbance position (Table 1). In



**Table 1** Time, linear escape distance and index of escape path of ten female GPS-collared moose in northern Sweden facing hunting disturbances during three approaches

Approach	Time (min)	Linear escape distance (m)	Index of escape path <sup>a</sup>
1	125±15	2888±330	0.54 ( <i>s</i> =28)**
2	174±41	3440±829	0.49 ( <i>s</i> =23)**
3	103±20	3013±712	0.62 ( <i>s</i> =23)**
Mean	133±16	3105±359	0.55

Linear escape distance is the path between initial disturbance position and where moose resettled after. The index of escape path is the ratio between the linear and the cumulative distance, Wilcoxon signed-rank test

\*\* $p<0.01$

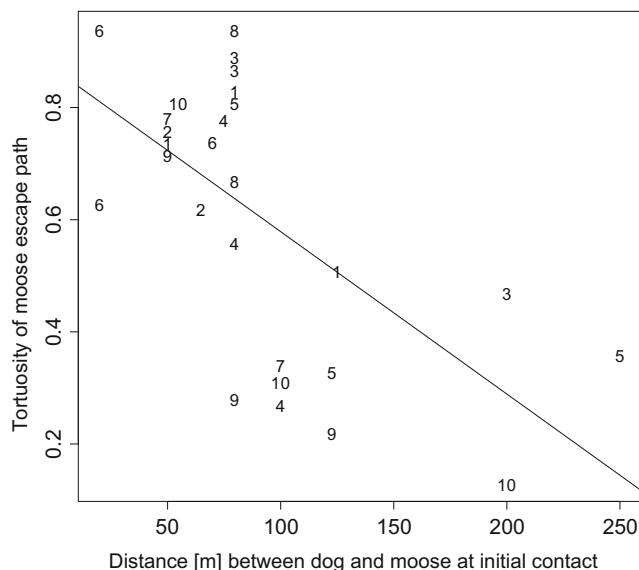
<sup>a</sup> 1=straight line; *s*=estimate given by the Wilcoxon signed-rank test

response to all three trials, moose responded by moving in a tortuous pattern to their resettle point. The shorter the distance between the dog and the moose was at the initial contact, the more straight moose escape path became ( $F_{1, 15}=-3.9$ ,  $p=0.001$ , Fig. 1). Our interpretation of Fig. 1 suggests a threshold value of 100 m which means if moose and dogs encountered each other at a closer distance, moose just ran off. The variance in moose escape path explained by difference among female moose was low (5 %), indicating similar behavioural response among moose females when approached by a hunting dog. Besides dog tracking time ( $F_{1, 17}=-2.6$ ,  $p=0.02$ ), no other covariate was correlated to the tortuosity of the moose escape path.

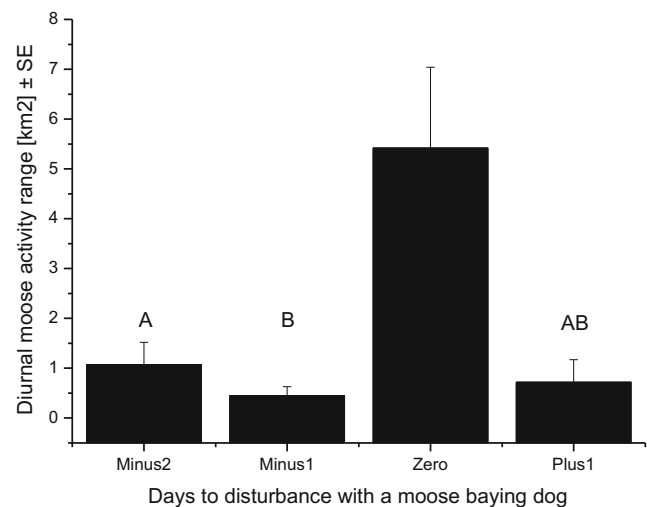
Our third prediction of greater movement activity when exposed to hunting was supported as well as moose were more active the first 2 h following initial disturbance (Fig. 2). We could also detect a short duration of increased movement activity coupled to the time the dog pursued a moose. Pursue time averaged  $46\pm 13$  min and did not differ among trials ( $F_{2, 14}=0.1$ ,  $p=0.9$ ).

We found no support for moose becoming less responsive to hunting activity among the three disturbance trials, neither in respect to changes in movement activity, time it took until moose resettled nor in the way how tortuous the escape paths were (*movement activity*:  $F_{2, 16}=1.6$ ,  $p=0.2$ ; *time until resettle*:  $F_{2, 19}=1$ ,  $p=0.4$ ; *sinuosity of escape path*:  $F_{2, 15}=0.05$ ,  $p=0.9$ ; Table 1).

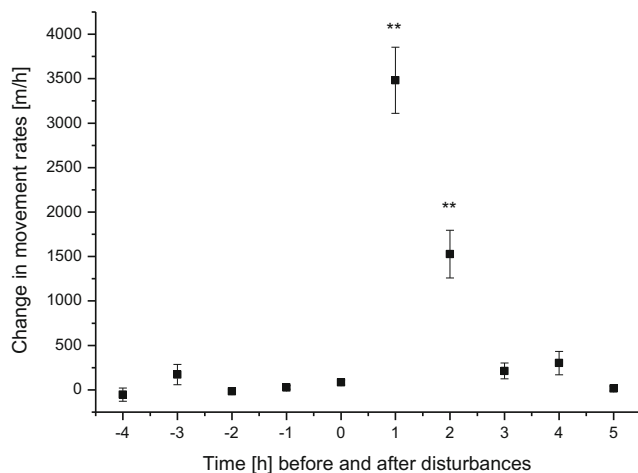
In line with our fourth prediction, size of diurnal activity ranges differed significantly ( $F_{3, 19}=19$ ,  $p<0.0001$ ; Fig. 3) in relation to time of disturbance. Ranges were enlarged at the day of treatment, were further apart and overlapped less after approach than before treatment (*centroids linear distance*  $1100\pm 343$  m (before) vs.  $3178\pm 819$  m (after),  $s=22$ ,  $p=0.03$ ; *overlap*  $10\pm 5$  % (before) vs.  $3\pm 2$  % (after),  $s=11$ ,  $p=0.03$ , Wilcoxon signed-rank test). All together, this confirms spatial displacement in response to hunting disturbance. Moose remained stationary after initial displacement the first 72 h following disturbance with no difference among the trials (*Distance over time*:  $F_{1, 116}=0.6$ ,  $p=0.4$ ; *trials*:  $F_{2, 17}=0.5$ ,  $p=0.6$ ).



**Fig. 1** Escape paths of ten female moose in boreal northern, Sweden. The graph is a function of distance (m) between dog and moose at the initial contact (linear-mixed model). Same number indicates the same moose



**Fig. 2** Change in moose movement rates (m/h) for ten female moose in northern Sweden before and following hunting disturbances. Letters indicate no significant difference ( $p<0.05$ )



**Fig. 3** Average size of moose 24-h ranges on the day of disturbance by hunting activity (day 0), 2 days before and 1 day after for ten female moose in boreal northern, Sweden. Same letters indicate non-significant difference ( $p < 0.05$ , adjusted  $p$  values Tukey post hoc test)

## Discussion

Our pilot study adds knowledge on the existence of multiple anti-predator strategies within a species, in this case for moose in an area currently wolf free but with human hunting as the dominating disturbance and mortality factor. Our finding suggests that female moose in a wolf-free area may have a mixed strategy among individuals, which will be beneficial for the adaptive capacity when eventually a new predator enters the system (Berger et al. 2001). Such multiple responses are previously shown for moose in south-central Sweden when bears recolonize and likely enhance the adoption to new conditions and increase survival when the behaviour spreads in the population (Berger et al. 2001). In this pilot study, we did document the majority of moose fled as predicted by theory and previous research (Sand et al. 2006). Moose shifted habitat after the experimental hunting disturbance. A novel suggestion from our study, worth following-up in future research, is that habitat and population density may determine an animal's response when, e.g. hunted. In our pilot study, moose living in closed terrain with moderate moose densities escaped in a manner that suggests increasing its chance to shake off its pursuer. More specifically, in areas with moderate to high moose density, escaping in a tortuous manner may increase the chance that the pursuing dog cross the trace of other moose, and thereby may switch tracking object considering the likelihood of other moose nearby. However, how moose escaped were correlated to the level of risk (i.e. moose-dog distance at first encounter and dog tracking time) supporting previous findings that the risk assessment largely affects prey escape response (Stankowich and Coss 2007). Other ungulates like, e.g. red deer, roe deer and wild boar seem to react as well to repeated hunting disturbance by dogs by altering vigilance, nocturnal activity and habitat shift (Jayakody et al.

2008; Bonnot et al. 2013; Thurfjell et al. 2013; Jarnemo and Wikenros 2014).

Natural predation by wolf, or hunting by humans with the help of a dog, may be driven by different trade-offs although utilizing similar strategies. Wolves are likely to face stronger selection pressure in predating the easiest prey available based on safety reasons and input effort; they therefore test actively their prey to assess its condition (Peterson et al. 1984). With an average chase distance of 76 m (majority less than 400 m), successful attacks by (Scandinavian) wolves are relatively short (Mech 1966; Peterson et al. 1984; Wikenros et al. 2009). In our experimental trials, moose that sensed the dog early moved straight away instead of fronting the attacker (e.g. Fig. 1) as the behaviour would have been in wolf areas. In that sense, there are some moose that are more vigilant than others—and thus not behave in a naïve way (Sand et al. 2006).

Yet being maladaptive when encountering wolves, to flee may be an advantageous strategy to adapt to when hunted by humans, and thereby resulting in predator facilitation in areas where predation by humans as well as by wolves occurs. Furthermore, the current low wolf to moose ratio which we estimate to circa 1:1000 (~400 wolves/400,000 moose) results in a low, geographically restricted encounter rate between Scandinavian wolves and moose (Eriksen et al. 2009, 2011). In contrast, the hunter to moose ratio is much higher 1:1.3 (~300,000/400,000). Thus, wolf predation risk is extremely low for a single moose individual compared with the risk of being killed during hunting (Eriksen et al. 2009) as every third moose is harvested. In turn, the relative lower importance of predation by wolves compared with human predation in Scandinavian moose is likely to be reflected in prey anti-predator response (Lima 1992). Recent results from south-central Sweden lend support to this low importance of wolf predation in relation to human hunting with dogs; Nicholson et al. (2014) suggest that moose does not shift habitat in wolf areas given the low chance of interactions between wolves and moose.

In our pilot study, 20 % of the individuals showed the alternative strategy of fronting the hunting dog which opens up for alternative predator-prey adjustments to spread when confronted with wolves (Berger et al. 2001; Sand et al. 2006). Equally interesting is that we found 80 % of the female moose individuals reacted in the same way, which we read as prevailing behavioural responses to the dominating hunting activity in our study area confirming previous finding in other study systems (Lima 1992; Crosmar et al. 2012; Nicholson et al. 2014). The consistency in moose response suggests behavioural adjustment towards the current dominant predator.

With a lifespan of up to 20 years for female moose in the absence of non-human predators and more than ten reproductive events during its life span, moose life history gives the precondition for learning and thus individual behavioural adjustments (Ericsson and Wallin 2001; Ericsson et al. 2001). Sweden implemented in 1967 a new moose-hunting regulation (SOU

2009). A central concept was that non-reproductive animals should be the preferred harvest whereas reproducing females should be spared. The normal situation after 1967 for a Swedish female moose with offspring was that the hunters started to select the calves but spared the reproductive, long-lived female. For the female, this experience could be viewed as sub-lethal but life-threatening interaction with its (human) predator. In turn and as a stage for lifetime learning, some surviving (but having lost her offspring) females may learn that the confrontation was a mistake and, thus, may be more prone to flee in future encounters, whereas others still would front the dog. Non-verified claims by the hunting community suggest that moose now compared to 40 years ago are drastically less prone to stop at bay when approached by a Norwegian elkhound.

Even though moose fled when approached, the tortuosity of their escape path and the relatively small linear distance between resettle point and initial disturbance position did not indicate high levels of stress in moose. Yet, a failure to relocate, despite disturbance, does not necessarily reflect a failure to perceive or respond to disturbance, but a lack of alternative habitats to switch to (Gill et al. 2001). Considering the landscape of fear, alternative undisturbed habitats devoid of humans, dogs and natural predators may indeed be limited during hunting season, in spite of plenty adequate habitat from a vegetation point of view. Moreover, the physical response may not tell the whole story (Bateson and Bradshaw 1997). Because risk of predation and escape behaviour affect prey physiological parameters (Creel et al. 2007), we consider wildlife physiological response to hunting activity to be of major interest and should be addressed in the future, particularly in heavily hunted game populations. Especially, ungulate species may be sensitive to degraded physiological parameters due to their close link between body condition and reproductive success (Sand 1996; Ericsson et al. 2001). Being beyond the scope of this pilot study, we recommend future studies to address behavioural plasticity in anti-predator behaviour. In moose, thus, the logical extension is the evaluation of moose behavioural response to both human and wolf predation where both predators co-exist and across different environments.

**Acknowledgements** We would like to thank the EU/Interregional IIIA project Moose in Midscandinavia, the Project of Moose Management in Västerbotten, the Program of Adaptive Management of Fish and Wildlife, the Swedish Association for Hunting and Wildlife Management and the Swedish Environmental Protection Agency for the financial support. We are grateful to Håkan Sand's and his groups for the discussions and knowledge transfer; E. Andersson and Å. Nordström for their help with the fieldwork; and N. Bunnefeld, J. Ball, S. Juthberg, H. Dettki and S. Gregory for the constructive comments on earlier versions of the manuscript.

**Author contributions** GE, WN and HD designed the data collection and experiments. WN and GE performed the experiments. WN, GE and HD analysed the data. GE and WN wrote the manuscript. HD provided the editorial advice.

## References

- Atwood TC, Gese EM, Kunkel KE (2009) Spatial partitioning of predation risk in a multiple predator-multiple prey system. *J Wildl Manag* 73:876–884
- Ballard WB, van Ballenberghe V (2007) Predator-prey relationships. In: Franzmann AW, Schwartz CC (eds) *Ecology and management of the North American moose*. Smithsonian Institution Press, Washington
- Baskin L, Ball JP, Danell K (2004) Moose escape behaviour in areas of high hunting pressure. *Alces* 40:123–131
- Bateson P, Bradshaw EL (1997) Physiological effects of hunting red deer (*Cervus elaphus*). *Proc R Soc Lond B* 264:1707–1714
- Berger J (2007) Carnivore repatriation and holarctic prey: narrowing the deficit in ecological effectiveness. *Conserv Biol* 21:1105–1116
- Berger J, Swenson JE, Persson IL (2001) Recolonizing carnivores and naive prey: conservation lessons from Pleistocene extinctions. *Science* 291:1036–1039
- Bonnot N, Morellet N, Verheyden H, Cargnelutti B, Lourtet B, Klein F, Hewison AM (2013) Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. *Eur J Wildl Res* 59:185–193
- Burnham KP, Anderson DR (2002) *Model selection and multi-model inference: a practical information-theoretic approach*. Springer-Verlag, New York
- Caro TM, Graham CM, Stoner CJ, Vargas JK (2004) Adaptive significance of antipredator behaviour in artiodactyls. *Anim Behav* 67:205–228
- Cederlund G, Kjellander P (1991) Effects of chasing by hunting dogs on roe deer. *Proc XXth Congr Int U Game Biol, Hungary*, pp 363–370
- Christianson D, Creel S (2008) Risk effects in elk: sex-specific responses in grazing and browsing due to predation risk from wolves. *Behav Ecol* 19:1258–1266
- Crawley MJ (2007) *The R book*. John Wiley and Sons, England
- Creel S, Christianson D, Liley S, Winnie JA (2007) Predation risk affects reproductive physiology and demography of elk. *Science* 315:960
- Creel S, Winnie JA, Christianson D, Liley S (2008) Time and space in general models of antipredator response: test with wolves and elk. *Anim Behav* 76:1139–1146
- Crosmary WG, Valeix M, Fritz H, Madzikanda H, Cote SD (2012) African ungulates and their drinking problems: hunting and predation risk constrain access to water. *Anim Behav* 83:145–153
- Danell K, Bergström R (2009) Mer vilt i dag än för 50 år sedan. *Vilt Och Fisk Fakta* 2009:4 (**In Swedish**)
- Eisenberg C, Hibbs DE, Ripple WJ, Salwasser H (2014) Context dependence of elk (*Cervus elaphus*) vigilance and wolf (*Canis lupus*) predation risk. *Can J Zool* 92:727–736
- Ericsson BioJobtjänst (2006) Älginventering från flyg i Malå–Gargnäs februari 2006 (Moose Aerial Survey Report in Swedish). 8pp
- Ericsson G, Wallin K (2001) Age-specific moose *Alces alces* mortality in a predator-free environment: evidence for senescence in females. *Ecoscience* 8:157–163
- Ericsson G, Wallin K, Ball JP, Broberg M (2001) Age-related reproductive effort and senescence in free-ranging moose *Alces alces*. *Ecology* 82:1613–1620
- Eriksen A, Wabakken P, Zimmermann B, Andreassen HP, Arnemo JM, Gundersen H, Milner JM, Liberg O, Linnell J, Pedersen HC, Sand H, Solberg EJ, Storaas T (2009) Encounter frequencies between GPS-collared wolves (*Canis lupus*) and moose (*Alces alces*) in a Scandinavian wolf territory. *Ecol Res* 24:547–557
- Eriksen A, Wabakken P, Zimmermann B, Andreassen HP, Arnemo JM, Gundersen H, Milner JM, Liberg O, Linnell J, Pedersen HC, Sand H, Solberg EJ, Storaas T (2011) Activity patterns of predator and prey: a simultaneous study of GPS-collared wolves and moose. *Anim Behav* 81:423–431

- Gill JA, Norris K, Sutherland WJ (2001) Why behavioural responses may not reflect the population consequences of human disturbance. *Biol Conserv* 97:265–268
- Jarnemo A, Wikenros C (2014) Movement pattern of red deer during drive hunts in Sweden. *Eur J Wildl Res* 60:77–84
- Jayakody S, Sibbald AM, Gordon IJ, Lambin X (2008) Red deer *Cervus elephus* vigilance behaviour differs with habitat and type of human disturbance. *Wildl Biol* 14:81–91
- Kreeger TJ, Arnemo JM (2007) Handbook of wildlife chemical immobilization. Terry J Kreeger, Wyoming
- Kuijper DPJ, de Kleine C, Churski M, van Hooft P, Bubnicki J, Jędrzejewska B (2013) Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. *Ecography* 36:1263–1275
- Lavsund S, Nygrén T, Solberg EJ (2003) Status of moose populations and challenges to moose management in Fennoscandia. *Alces* 39:109–130
- Lima SL (1992) Life in a multipredator environment—some considerations for anti-predatory vigilance. *Ann Zool Fenn* 29:217–226
- Littell RC, Milliken GA, Stroup WW, Wolfinger RD, Schabenberger O (2006) SAS for mixed models. SAS Press, USA
- Mech LD (1966) The wolves of Isle Royale. U.S. National Park Service. Fauna of the National Parks of the U.S. Fauna Series 7
- Nicholson KL, Milleret C, Månsson J, Sand H (2014) Testing the risk of predation hypothesis: the influence of recolonizing wolves on habitat use by moose. *Oecologia* 1–12. doi:10.1007/s00442-014-3004-9
- Peterson RO, Woolington JD, Bailey TN (1984) Wolves of the Kenai Peninsula, Alaska. *Wildl Monogr* 88:1–52
- Proffitt KM, Grigg JL, Hamlin KL, Garrott RA (2009) Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. *J Wildl Manag* 73:345–356
- Ripple WJ, Betscha RL (2012) Large predators limit herbivore densities in northern ecosystems. *Eur J Wildl Res* 58:733–742
- Samia DS, Nomura F, Blumstein DT (2013) Do animals generally flush early and avoid the rush? *Biol Lett* 9:20130016
- Sand H (1996) Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity and environmental conditions. *Oecologia* 106:212–220
- Sand H, Wikenros C, Wabakken P, Liberg O (2006) Cross-continental differences in patterns of predation: will naïve moose in Scandinavia ever learn? *Proc R Soc B* 273:1421–1427
- Sand H, Wabakken P, Zimmermann B, Johansson Ö, Pedersen HC, Liberg O (2008) Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates? *Oecologia* 156:53–64
- Singh NJ, Börger L, Dettki H, Bunnefeld N, Ericsson G (2012) From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. *Ecol Appl* 22:2007–2020
- SLU (2014) Moose management. Home page [www.slu.se/en/collaborative-centres-and-projects/moose-management/](http://www.slu.se/en/collaborative-centres-and-projects/moose-management/). Accessed 4 Aug 2014
- Solberg EJ, Loison A, Saether BE, Strand O (2000) Age-specific harvest mortality in a Norwegian moose *Alces alces* population. *Wildl Biol* 6:41–52
- SOU (2009) Uthållig älgförvaltning i samverkan. Governmental White Paper on Moose Management 2009:054. (In Swedish)
- Stankowich T (2008) Ungulate flight response to human disturbance: a review and meta-analysis. *Biol Conserv* 141:2159–2173
- Stankowich T, Coss RG (2007) Effects of risk assessment, predator behavior, and habitat on escape behavior in Columbian black-tailed deer. *Behav Ecol* 18:358–367
- Statistics Sweden (2008) Swedish centre for statistical information about demographic data. [www.scb.se](http://www.scb.se). Accessed 27 Jul 2008
- Swedish EPA (2014a) Population estimates and distribution of large carnivores in Sweden. [www.naturvardsverket.se](http://www.naturvardsverket.se). Accessed 6 Aug 2014
- Swedish EPA (2014b) Hunting in Sweden; hunting permits. [www.naturvardsverket.se](http://www.naturvardsverket.se). Accessed 6 Aug 2014
- Swedish Land Survey (2008) Maps about land cover, elevation and infrastructure data. <http://www.lantmateriet.se>. Accessed 11 Sept 2008
- Swenson JE, Sandegren F, Bjärvall A, Soderberg A, Wabakken P, Franzén R (1994) Size, trend, distribution, and conservation of the brown bear *Ursus arctos* population in Sweden. *Biol Conserv* 70:9–17
- Swenson JE, Dahle B, Busk H, Opseth O, Johansen T, Söderberg A, Wallin K, Cederlund G (2007) Predation on moose calves by European brown bears. *J Wildl Manag* 71:1993–1997
- Thurfjell H, Spong G, Ericsson G (2013) Effects of hunting on wild boar *Sus scrofa* behaviour. *Wildl Biol* 19:87–93
- Wabakken P, Sand H, Liberg O, Bjärvall A (2001) The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978–1998. *Can J Zool* 79:710–725
- Wikenros C, Sand H, Wabakken P, Liberg O, Pedersen HC (2009) Wolf predation on moose and roe deer: chase distances and outcome of encounters. *Acta Theriol* 54:207–218
- Wikenros C, Kuijper DPJ, Behnke R, Schmidt K (2015) Behavioural responses of ungulates to indirect cues of an ambush predator. *Behaviour*. doi:10.1163/1568539X-00003266